Review of shell reduction and loss in traditional and phylogenetic molluscan systematics, with experimental manipulation of a negative gain character

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Abstract: Modern phylogenetic methods are improving our basis for molluscan systematics and our understanding of evolutionary processes. The use of traditional characters in a phylogenetic analysis helps us directly contrast their accustomed "taxonomic value" with synapomorphies suggested by a cladogram. While most cladistic characters are structurally complex, opisthobranch and pulmonate gastropods exhibit numerous characters which are losses - in shell, operculum, radula, etc. - some as presumed synapomorphies for higher-level taxa. These losses, called negative gains, can be complete (absence) or partial (reduction). To describe and code such characters, we are forced to assess morphology that is not observable. How we do so can affect tree topology, and thus the final hypothesis. This in turn determines what sequences of character evolution are supported, what monophyletic clades are recognized, and if translated into a hierarchical classification, what established taxa are confirmed or rejected. Negative gain characters must be explicitly defined to ensure repeatability; in particular, "reduced" must consider the type of reduction (in size or composition), the level of reduction (expressed qualitatively or numerically), and presumed homologies of an unobservable feature. Inclusion of negative gain characters in an analysis can document the extent of putative parallelism or "trends" for character loss in a lineage; still, subjective coding decisions have profound effects. These points are illustrated here by three datasets derived from recent literature, on sacoglossan and notaspidean opisthobranchs and on sigmurethran pulmonates, in which the shell exists in fully present, reduced, and fully absent states. By manipulating only shell characters in these multi-system datasets, through different *a priori* assumptions and coding alternatives (binary, multistate unordered, multistate ordered, uncoded/mapped), changes in the resulting cladogram(s) were induced, ranging from extreme, to slight, to unchanged. In the absence of methodological preference, the use of multiple methods is advised, with conclusions based on all results and on confidence in carefully coded characters.

Key words: cladistics, classification, Mollusca, Opisthobranchia, Pulmonata

In the last decade of systematic malacology, phylogenetic methodology (= cladistics) has allowed the re-evaluation of traditional molluscan systematics in ways that are more objective and repeatable than previously possible. Although the advantages of this technique are now well-accepted, cladistic analyses often suggest dramatically different evolutionary relationships, and thus hierarchical taxonomic classifications, than those long-considered as dogma. Because ranked classifications are necessary means of convenience and communication, radical changes from familiar taxonomic arrangements can place the phylogeneticist at odds with workers in applied systematics (*e. g.* education, ecology, collection management, biopolitics) as well as other disciplines (*e. g.* neurophysiology), needing proper labels for their research subjects. The systematic research community is likewise impacted when newly-named taxa, created in a fervor to label clades, are rapidly overturned, often by the same author(s) (*e. g.* Triganglionata Haszprunar, 1985b = Allogastropoda Haszprunar, 1985a). It is therefore prudent to be confident of cladistic results before traditional arrangements are summarily discarded in favor of phylogenetic ones.

Whenever cladistic revision of a taxonomic group is attempted, two questions must be addressed: (1) are the traditional taxa monophyletic clades? and (2) are the traditional taxon-defining characters synapomorphies? The most effective method of answering both of these questions is to actually code and use traditional characters as part of the phylogenetic dataset. Only by doing so can the accustomed "taxonomic value" of a character be directly compared with the pattern of character evolution revealed by a cladogram.

Cladistics depends on the inheritance of derived characters, and performs optimally when these characters are structurally complex. But in many traditional characters of many taxa, the derived condition is absence (= presumed secondary loss of a primitively present feature) and is called a negative gain. In cladistic terms, instead of plesiomorphic 0 = absent, and derived 1 = present, one has the reverse: 0 = present, 1 = absent. Difficulties are compounded when an intermediate stage is involved, *i. e.* when the feature is still present but appears reduced or simplified in some fashion. The intermediate state changes the character

from discrete (present/absent) to continuous (coded as 0 = present, 1 = reduced, 2 = absent), wherein the character state boundaries (especially between present and reduced) can be ambiguous.

Traditional systematics is replete with examples of taxa defined (at least in part) by derived absences, *e. g.* reptiles without limbs (Serpentes; snakes). Among mollusks, Ponder and Lindberg (1997: 205) suggested that "loss of plesiomorphic structures, rather than their structural modification, accounts for much of the homoplasy seen in gastropods." Examples of traditional taxonomic losses across the phylum include the entire jaw/radula complex in Bivalvia, ctenidia in Scaphopoda and Heterobranchia, the operculum in Marginellidae and most Olividae, the radula in Pyramidellidae and Retusidae, and jaws in Neogastropoda (see Boss, 1982; Willan, 1987; South, 1992; Salvini-Plawen and Steiner, 1996). Nearly half of the traditional taxonomic characters of Cephalaspidea (Opisthobranchia; "bubble snails") involve reduction or loss (= total reduction) of a feature (Mikkelsen, 1993). Reduction of the shell is probably the most-cited example, and has presumably occurred many times throughout the course of molluscan evolution. Reasons proposed for such losses include: ecophenotypic (streamlining for burrowing, flexibility for slithering into crevices), physiological (scarcity of calcium in the environment, constraints of parasitic life), and developmental (miniaturization, paedomorphosis). [Fong *et al.* (1995: 251) suggested that loss might have less to do with adaptation than with "indirect selection" when there is "relaxation of ... stabilizing selection" on a character; they viewed the reductive process as evolutionarily polarized, from nonfunctionality, through atrophication, to complete loss.] Regardless of the actual underlying cause, when shell reduction is considered "an evolutionary trend" or characteristic of a taxon, it becomes a negative gain character in cladistics.

Although negative gain characters are not impossible to accommodate in cladistics, they can be "especially problematic" (Bieler, 1992: 315; Mikkelsen, 1993). First, because homology centers on structure for recognizing homologous states of a character (by at least one definition; see reviews by Hall, 1994), negative gains are more difficult to code because there is nothing (in the case of absent features) to interpret. Second, because the term "reduced" can encompass a broad range of factors (reduced in size, thickness, sculpture, complexity, function, etc.; Pogue and Mickevich, 1990; Proctor, 1996), one must assure that the reduced state of one taxon is the same (homologous?) with that of the other taxa being investigated; thus precise definition of kind and amount of reduction is required. Third, how we code absence is controversial: although unknown or inapplicable character states are most often treated as question marks in datasets, Pimentel and Riggins (1987) advocated that absence is a valid character state when it is apomorphic. Finally, because reduction or loss of a feature can conceivably occur more than once in a lineage, negative gains carry the threat of increased homoplasy (= extra steps in an analysis, reflected in a character consistency index of < 1.0). So, negative gain characters raise recurrent uncertainties about: (1) homology (is the present feature homologous with the absent feature?), (2) definition (how do we describe something we can't see?), (3) procedure (how do we code absence and/or reduction?), and (4) relative usefulness (should we omit such characters from the analysis if they are inherently homoplastic?).

Focussing on the molluscan shell, the goals of this study are: (1) to review shell reduction and loss as an example of a traditional qualitative character in mollusks; (2) to discuss how shell reduction and loss can be used as a negative gain character for cladistic analysis, in terms of implied homologies, requisite definition, and inherent difficulties; (3) using published datasets, to show how results and conclusions can change with experimental manipulation of shell reduction and loss characters; (4) to consider the pros and cons of coding and analytical alternatives; and (5) to emphasize the cladistic utility of negative gain characters, as means of hypothesizing the occurrence of homoplasy and testing accustomed taxonomic value.

DEFINITION AND REVIEW OF SHELL REDUCTION

A large external shell composed of calcium carbonate and secreted by the mantle is synapomorphic for, and thus plesiomorphic within, conchiferan mollusks (Brusca and Brusca, 1990; Lindberg and Ponder, 1996). Absence (= loss) of the shell is therefore apomorphic within the group (Ponder and Lindberg, 1997). Ontogenetic evidence supports this interpretation; a shell is present in the larval form of most shell-less mollusks. Loss of the adult shell has presumably occurred in parallel in octopod Cephalopoda and a number of times in two major gastropod lineages: Opisthobranchia (including some Anaspidea, Notaspidea, and Sacoglossa, and all Nudibranchia and Gymnosomata; see Gosliner and Ghiselin, 1984; Gosliner, 1991), and Pulmonata (including especially Soleolifera and Philomycidae; see South, 1992). Opisthobranchs are most renowned in this regard; as noted by Solem (1974: 117), "The one clear trend in evolution [of opisthobranchs] is toward loss of the shell."

Several lineages of mollusks show "the most clearly defined trend in shell variation" (Solem, 1974: 16) where the derived loss is less than complete, *i. e.* where the shell is present but reduced. A reduced (= vestigial, rudimentary) shell is listed as a traditional character for higher taxa from

the subclass (*e. g.* Opisthobranchia) to family (*e. g.* Teredinidae) level (Table 1). However, shell reduction can encompass: (1) reduced in size relative to the overall size of the body (also generally meaning that the mollusk cannot fully retract into its shell), and/or (2) reduced in thickness, *i. e.* thin-walled, fragile, and/or weakly calcified. While not qualifying as shell reduction alone, other recurring attributes of reduced shells include: (1) auriculiform or plate-like shape, with an oversized body whorl (= rapidly expanding whorls), and enlarged aperture; (2) streamlined with regard to reduction in spines, ribs, and other sculpture; and (3) completely internal or incompletely internalized by hypertrophied, overlying mantle folds.

Evolutionary modification from shell present to reduced, then, can represent different evolutionary pathways, and caution must be used that one is coding only one kind of reduction within a single transformation series. For example, the large, paper-thin shell of a *Haminoea* (Opisthobranchia: Cephalaspidea: Haminoeidae) and the small, thick one of a *Fissurellidea* (Vetigastropoda: Fissurellidae) can both be called reduced, therefore theoretically they could both be identically coded. Yet the character state change is not identical - one is reduced by becoming thinner, the other by becoming smaller. In most taxa, the shell is actually reduced in both size and thickness (Table 1). Thus the transformation is a mixture of two different evolutionary pathways that can occur together or independently. Although the shell itself is homologous within Mollusca, the reduced state of one shell might not be homologous with the reduced state of another. Likewise the absent state of one shell (*e. g. Bursatella*, an anaspid) is not necessarily homologous with the absent state of another (*e. g.* a nudibranch). Proctor (1996: 144) recognized this problem by stating that "losses of a character state may be falsely homologized, since although there may be many independent losses of a character state, seldom are there structural or behavioral clues to this independence." In-depth examination of molluscan larval shells, which are present in nearly all shell-less groups (Thompson, 1976), could provide ontogenetic evidence for decision-making in this area.

Table 1. Supraspecific taxa listing "shell reduced" [but not meaning "absent"] as a traditional character. Based on descriptions by Boss (1982) unless otherwise noted. (S, reduced in size; T, reduced in thickness).

"Prosobranchs"	
Fissurellidae: *Fissurellidea* group (McLean, 1984)	S
Naticidae: Sininae	ST
Lamellariidae	ST
Carinariidae	ST
Opisthobranchs	
Cephalaspidea	ST or T
Runcinoidea	ST
Philinoglossacea	ST
Sacoglossa: Oxynoidae	ST
Anaspidea: Notarchidae	ST
Notaspidea	S
Pulmonates	
Amphibulimidae	ST
Limacidae	S
Testacellidae	S
Bivalves	
Galeommatoidea	ST or T
Teredinidae	S
Cephalopods	
Coleoidea (also Brusca and Brusca, 1990)	ST
Teuthoidea (also Brusca and Brusca, 1990)	ST
Loliginidae	ST
Octopoda (also Brusca and Brusca, 1990)	ST
Cirrata	ST
Opisthoteuthidae	ST
Incirrata	ST
Boltaenidae	ST

In addition to defining the pathway of reduction, the limits of reductive character states must be clearly defined. How much smaller or thinner does the shell have to be, to be coded as reduced rather than as fully present? Will levels of reduction be coded as separate character states, and if so, are these meaningful levels, or arbitrary cut-offs within a continuous morphocline? Several solutions have been utilized in the past: capacity of the animal to withdraw into the shell (Boss, 1982); and relative sizes of the shell and mantle, expressed qualitatively or as a numerical ratio (McLean, 1984; Willan, 1987; Bieler and Mikkelsen, 1992).

In summary, for coding and analyses to be repeatable, defining the shell condition (*i. e.* the kind and degree of reduction) is a fundamental step. To minimize *a priori* reasoning, shell condition must be as explicitly defined as possible, ideally without the use of imprecise terms such as vestigial or rudimentary.

CODING ALTERNATIVES AND METHODS

In this study, published datasets were used to illustrate if and how a change in coding adult shell reduction can produce different results. For these purposes, I am assuming that reduction has been in each case rigorously defined as required above, limiting the reduced state to one homologous pathway and one level. In each case dataset, four alternative coding choices are used, reflecting different *a priori* assumptions and phylogenetic philosophies.

Binary Coding (two separate binary characters: (1) 0 = present, 1 = absent; and (2) 0 = fully present, 1 = reduced): In this method, taxa with shells absent (character 1 = 1) are coded "?" (= unknown or inapplicable) for character 2 because the appearance of something that is not present cannot be determined (Maddison, 1993). [This is not

the same as additive binary coding, which divides a multistate character into subcharacters and produces the same cladogram as additive (= ordered) multistate character (Hauser and Presch, 1991; Wiley *et al.*, 1991).]

Multistate Unordered Coding (single multistate character: 0 = fully present, 1 = reduced, 2 = fully absent): This coding avoids the "?"s necessary with Binary Coding (above). All characters were treated as fully unordered (= non-additive, minimally connected), that is, considering any character state change (0 to 1, 1 to 2, 0 to 2, plus reversals) as possible in a single step.

Multistate Ordered Coding: Same coding as the previous, but this character (only) was treated as a linearly ordered character (= additive, maximally connected). This assumes that reduced is a requisite intermediate stage between fully present and fully absent, therefore, *e. g.* a change from 0 to 2 requires two steps instead of one. All other multistate characters in each dataset were left unordered.

Uncoded/Mapped: Here shell condition was not coded or used in the analysis, but was subsequently mapped onto the resultant tree(s). This method has been used by authors when data are missing in a large number of taxa (Mikkelsen, 1996), or when negative gain characters are thought to be overly homoplastic (Ponder and Lindberg, 1996, 1997; although one survey [Proctor, 1996] found that potential homoplasy has seldom been cited as a reason to exclude characters). This reflects a decision, *a priori,* not to allow the character to play a role in tree construction.

Each trial or test dataset, then, consisted of four analyses: Binary Coding, Multistate Unordered Coding, Multistate Ordered Coding, and Uncoded/Mapped. Each used the parsimony-based algorithms of Hennig86 (Farris, 1988), using in each trial an algorithm which resolved in a reasonable amount of time and yielded a total number of trees which could be rapidly analyzed (i. e. no memory overflows). Because this is a demonstration, it was not important that these be rigorous analyses, only comparable ones. The same algorithm was used within each trial set of four analyses; all characters were given equal weight (= unweighted) in all analyses. Uncoded/Mapped analyses used the binary datasets, but with shell-reduction characters inactivated within Hennig86. Character analysis was assisted using Clados (Nixon, 1992). Cladograms were rendered for publication using Component (Page, 1993).

Cladistic analyses most often result in more than one, often many, most-parsimonious trees (MPTs). Although "one would ideally examine the implications for character evolution on all equally acceptable phylogenies" (Maddison, 1991: 315), most authors condense the MPTs either through consensus trees or successive approximations weighting (Carpenter, 1988). Because these decrease the amount of information revealed by the analysis, an alternative method of summarizing topologies was used here. When a series of taxa occur in a consistent region of all trees, but in varying arrangements within that region, repetitive regional topologies can be identified that are much smaller in number than the total number of trees. Each regional topology can be examined separately for implied patterns of character evolution. For this discussion, only those regions in which character state changes relevant to shell reduction or loss occurred are presented in full. Other regions are abbreviated here, and the arrangement of taxa comprising each such region (although admittedly not unimportant to tree length and construction) was generally disregarded.

TEST DATASET RESULTS

Although manipulation of hypothetical datasets in studies such as these are often instructive, one is inevitably left wondering how similar manipulations would affect real data. Therefore, the early choice was made here to conduct these trials on actual datasets. Unfortunately, very few published datasets have used shell reduction and loss as coded characters, perhaps for the reasons cited above. Some studies have included a shell present/reduced character (*e. g.* Bieler and Mikkelsen [1992] coded 0 = subequal to mantle, 1 = significantly smaller than mantle; Jensen [1996a] used 0 = large, 1 = small), but to be most effective here, datasets using taxa with shells in at least three possible states (present/reduced/absent) were desired. Experimental results using three test datasets are here presented: sacoglossan (Jensen, 1996b) and notaspidean opisthobranchs (Willan, 1987), and sigmurethran pulmonates (Tillier, 1989). Each dataset included characters from a wide range of soft anatomy systems (*e. g.* mantle cavity, alimentary tract, nervous system, reproductive system) in addition to the shell characters. Summaries of the results in each section (below) emphasize: the number of MPTs, monophyletic clades supported (including traditional taxa, for ease of discussion), and interpretation of shell reduction/loss evolution from the cladogram(s). NOTE: Although these experimental trials used real datasets, the object was neither to revise the results of the original published version nor to criticize the original analysis. These matrices were analyzed here as experimental datasets for demonstration purposes only, and these results should not be interpreted as rigorous phylogenetic reanalyses of taxa. Support for named clades is mentioned only to illustrate changes in result depending on coding alternative used.

SACOGLOSSAN OPISTHOBRANCHS

The opisthobranch subgroup Sacoglossa (= Ascoglossa, "leaf-slugs") includes members with full-sized

shells, others with shells reduced in size (both of these categories are reduced in thickness), and many without shells as adults. Shell presence/absence has played a traditional role in sacoglossan classification, with two groups, Oxynoacea and Placobranchacea, containing shelled and unshelled forms, respectively.

In 1996, Jensen published a phylogenetic analysis of the Sacoglossa, including 35 ingroup taxa (mostly at genus-level) and 52 characters from the shell, mantle cavity, gross morphology, circulatory, digestive, reproductive, and nervous systems, and egg mass. Her dataset (Jensen, 1996b: table 4) included five taxa with fully present shells, three with reduced shells, and 27 without shells as adults. Her character list treated the shell using three binary characters: (1) 0 = present, 1 = absent; (2) 0 = univalved, 1 = bivalved; and, (3) 0 = covering whole body, 1 = reduced. Character 2 accomodated shell condition in the famous "bivalved gastropods" (*Julia, Berthelinia*) and was not manipulated here. Characters 1 and 3 reflect shell loss or reduction in size, and were those involved in manipulation. Because Jensen's character list and data matrix (Jensen, 1996b: tables 3-4) were used here largely unchanged from the published version (altered only by adding an all-zero character 0 and correcting character 21 for *Mourgona* to 0; K. R. Jensen, pers. comm., 1996), they are not reproduced here.

The Hennig86 algorithms *mhennig** and *bb** (multiple passes plus branch-swapping) were used for these analyses. Several monophyletic clades were consistent and are abbreviated here for discussion: (1) 27 unshelled taxa hereafter combined as Placobranchacea; (2) the bivalved gastropods, *Julia* + *Berthelinia*, hereafter abbreviated as Juliidae; and (3) *Oxynoe* + *Lobiger* + *Roburnella* (usually united as a clade), hereafter (when monophyletic) as Oxynoidae. Variation within monophyletic Oxynoidae was disregarded, as was one taxon, *Cylindrobulla*, which was consistently basal and unresolved with the outgroup (Jensen's "Ancestor").

Binary Coding. Analysis of the original dataset produced 56 MPTs of length 155 (CI 0.41, retention index [RI] 0.76). These fell into eight topologies (Figs. 1-8: 1, 14 MPTs; 2, 12 MPTs; 3-5, eight MPTs each; 6-8, two MPTs each). Shell reduction (character 3 = 1) occurred independently of shell loss (character 1 = 1) (*i. e.* a branched character state tree) in six of the eight topologies (Figs. 3-8, 30 of 56 MPTs, or 54%). However, in spite of independent binary coding, shell reduction was prerequisite to shell loss (*i. e.* a linear character state tree) in the remaining two topologies (Figs. 1-2), which included the most frequently-occurring topologies (14 and 12 MPTs, respectively) and nearly half of the MPTs (26 of 56, or 46%). The traditional Oxynoacea was supported by four topologies (Figs. 5-8, 14 MPTs or 25%).

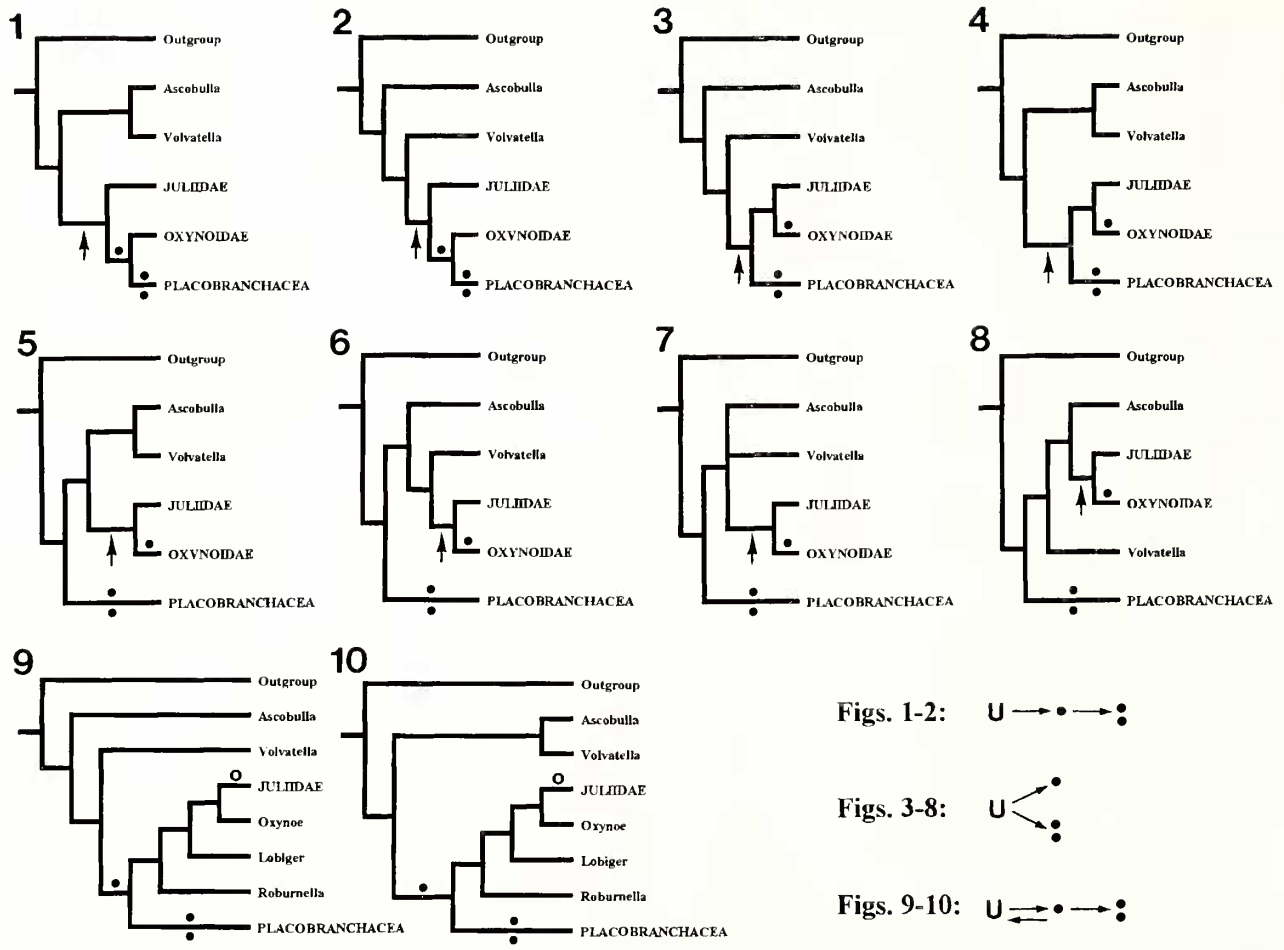
Multistate Unordered Coding. This method combined binary characters 1 and 3 to form a single multistate shell character: 0 = present, 1 = reduced, 2 = absent. The combined character replaced character 1, and character 3 was thus eliminated. The algorithm likewise produced 56 MPTs, in the same topologies as Binary Coding, and of nearly identical statistics (length 155, CI 0.41, RI 0.75). Character state trees were therefore also unchanged from Binary Coding.

Multistate Ordered Coding. Using the same dataset as Multistate Unordered Coding, this analysis was run with character 1 (only) ordered. 26 MPTs resulted, of length 155 (CI 0.41, RI 0.76). The result comprised only two topologies, identical in form (Figs. 1-2) and number (14 + 12 MPTs, respectively) to those requiring shell reduction prerequisite to loss in the previous two analyses (*i. e.* only those with linear character state trees). Unlike the previous two cases, traditional Oxynoacea was not supported by any of the resultant trees.

Uncoded/Mapped. This analysis used the original (binary) dataset, but with characters 1 and 3 inactivated. The result was 60 MPTs of 153 steps (CI 0.40, RI 0.75), including 56 trees of the same eight topologies realized by the previous analyses (Figs. 1, 14 MPTs; 2, 12 MPTs; 3-5, eight MPTs each; 6-8, two MPTs each), plus two new topologies (Figs. 9-10, two MPTs each). In these two new topologies (Figs. 9-10), the Oxynoidae became unresolved (apparently in the absence of its single synapomorphy, shell reduced [it was also united by two homoplastic character state changes in the nervous system]).

When mapped onto the trees, shell loss remained synapomorphic for the Placobranchacea, in evidence of support for the clade by three other synapomorphies (in vascular and reproductive characters) plus other homoplastic character state changes (in the nervous system). Shell reduction was independent of shell loss in 30 MPTs (Figs. 3-8, 50%); reduction was prerequisite to loss in the remaining 30 MPTs (50%), including the two new topologies (Figs. 9-10) and, again, the most frequently-occurring topologies (Figs. 1-2). Notably the two new topologies (Figs. 9-10) required reversals in shell reduction, from shell reduced back to fully present in Juliidae. Traditional Oxynoacea was supported by four topologies (Figs. 5-8, 14 MPTs or 23%).

Summary. (1) Change in coding from binary to multistate produced no change in the results if the analysis was run unordered. Ordering the shell reduction/loss character resulted in fewer MPTs, restricted to those which required shell reduction as an intermediate step before shell loss; in this case, this was a subset of the Binary or Multistate Unordered Coding results. Eliminating the shell reduction/loss characters produced more MPTs than any other coding alternative. (2) Regardless of coding alterna-

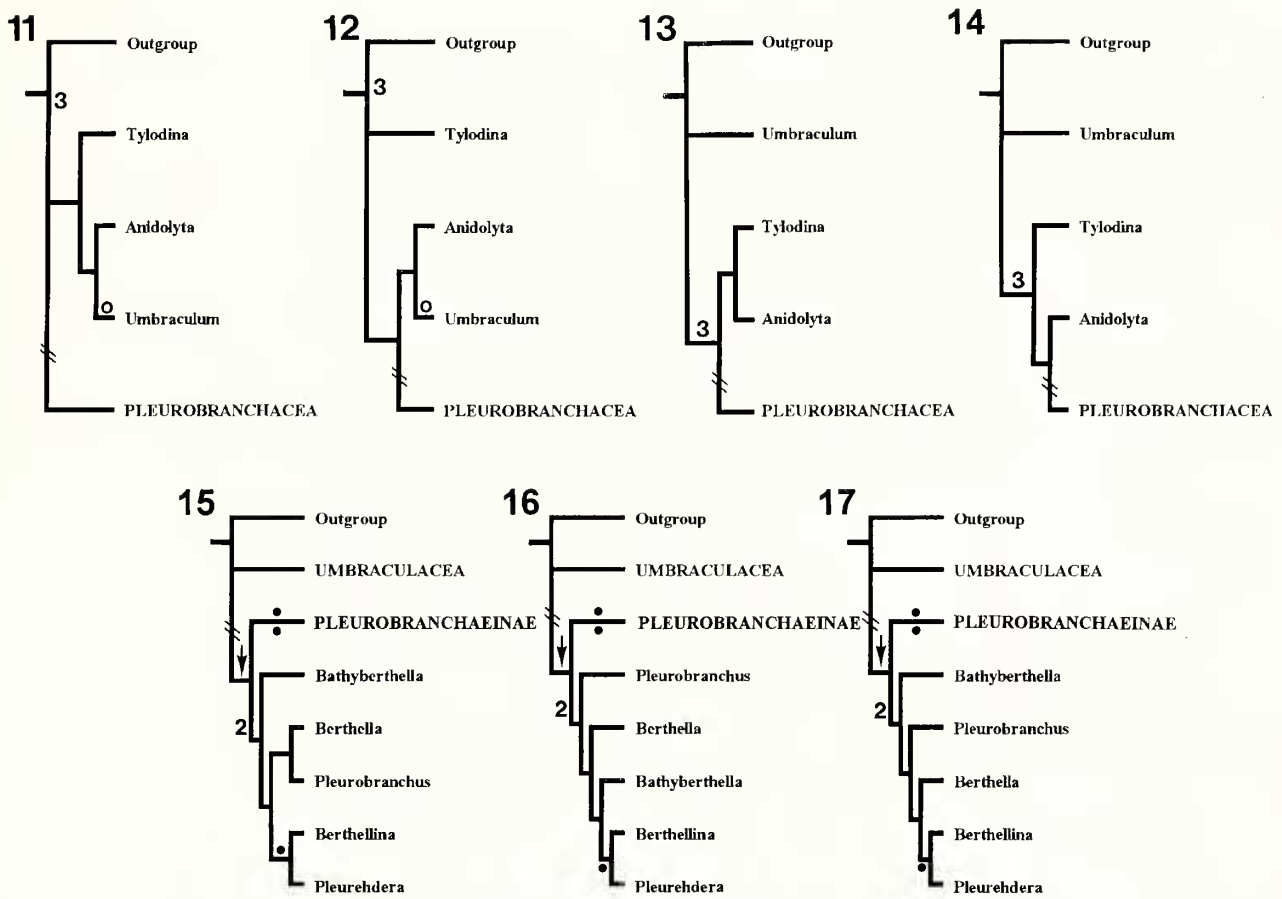


Figs. 1-10. Sacoglossan opisthobranch test dataset results and character state trees. Figs. 1-8. Most-parsimonious tree topologies from Binary, Multistate Unordered, and Multistate Ordered Coding. Figs. 9-10. Same, from Uncoded/Mapped results. (•, shell reduction; ••, shell loss; o, reversal to shell fully present; arrow, position of shell reduction if Juliidae shell is reduced before becoming bivalved [see text]).

tive, identical traditional taxa were generally supported. Placobranchacea consistently formed a clade even if shell reduction/loss was eliminated from tree construction. Oxynoacea was supported by most MPTs, but was unresolved in two topologies where shell reduction/loss characters were eliminated. (3) Regardless of coding alternative, shell reduction/loss characters usually served as synapomorphies for various clades: shell absent for Placobranchacea, and shell reduced for Oxynoidae (most cases). (4) Regardless of coding alternative, tree topology was generally sustained, even in Uncoded/Mapped analyses. (5) Shell reduction was prerequisite to shell loss in about 50% of the MPTs produced by each analysis, and in the most-frequently occurring topologies of each analysis. This was true even in unordered analyses. (4) Reversals occurred only in the Uncoded/Mapped analysis, involving only the Juliidae regaining a fully present shell from the reduced shell of Oxynoacea. This hypothesis could be envisioned if the bivalved gastropod shells of Juliidae could only be derived from a reduced shell; Kay (1968) in fact noted the close "approximation" of a single juliid valve to the reduced shell of *Lobiger*. It is interesting to note that the node at which shell reduction occurred can be easily shifted in each tree to accommodate the Juliidae (Figs. 1-8, arrows); if this is done, shell reduction becomes prerequisite to shell loss in two more topologies (Figs. 3-4), with reflective shifts from branched to linear character state trees.

NOTASPIDEAN OPISTHOBRANCHS

Willan (1987) published one of the first phylogenetic analyses involving opisthobranchs, in his investigation of the Notaspidea (= Pleurobranchomorpha, "side-gilled slugs"). Here again, condition of the shell has played a traditional role in classification (Boss, 1982; Marcus, 1984, 1985), including forms with external cap-shaped shells (Umbraculacea), and those with reduced or absent



Figs. 11-17. Notaspidean opisthobranch test data results. Figs. 11-14. Most-parsimonious tree topologies, basal region. Figs. 15-17. Same, top region. (2, shell internalization; 3, shell decalcification; •, shell reduction; ••, shell loss; o, reversal to shell calcified (character 3); arrow, position of shell internalization (character 2) if Pleurobranchaeinae are included; double slash, demarcation between basal and top tree regions).

shells (Pleurobranchacea: Pleurobranchidae: Pleurobranchinae [reduced in some] and Pleurobranchaeinae [lost in all]).

Willan's (1987: tables 3-5) original dataset included characters of the shell, mantle cavity, head-foot, digestive system, and reproductive system. The 57 characters in 11 genus-level taxa (Willan, 1987: table 5) included four binary shell characters: (1) 0 = present, 1 = absent; (2) 0 = external, 1 = internal; (3) 0 = calcified, 1 = uncalcified; and (11) 0 = mantle and shell subequal in size, 1 = mantle larger than shell. While characters 2 and 3 are attributes commonly noted in reduced shells (see above), characters 1 and 11 are expressions of shell loss and reduction, respectively, and were the only ones manipulated here. Following minor modifications to facilitate the parsimony-based Hennig86 analysis (see Notes in Table 2), the resulting list of 41 characters (Table 2) was subjected to the exhaustive Hennig86 algorithm, *ie** (implicit enumeration).

Each analysis produced the same number of trees (12 MPTs) of comparable length and tree statistics, with repetitive topology in two regions. The basal part of the tree, including the taxa of traditional Umbraculacea (*Tylodina, Anidolyta*, and *Umbraculum*), appeared in four topologies of three MPTs each (Figs. 11-14). Traditional Tylodinidae (*Tylodina* + *Anidolyta*) and Umbraculacea formed monophyletic clades in only one topology or three MPTs (25%) each (Figs. 13 and 11, respectively).

The "top" of the tree, comprising the eight taxa of Pleurobranchacea (and Pleurobranchidae) consistently placed the two traditional subfamilies, Pleurobranchaeinae and Pleurobranchinae, as monophyletic sister-groups. The three taxa of Pleurobranchaeinae (*Pleurobranchella* + *Pleurobranchaea* + *Euselenops*) formed a consistent monophyletic clade, hereafter combined as Pleurobranchaeinae. The five taxa of Pleurobranchinae (*Bathyberthella* + *Berthella* + *Pleurobranchus* + *Berthellina* + *Pleurehdera*) appeared in three topologies of four MPTs each (Figs. 15-17). Within this, *Berthellina* + *Pleurehdera* formed another consistent monophyletic clade (traditionally unnamed).

Shell absent (character 1 = 1) was consistently

Table 2. Notaspidean taxon list (with shell condition), character list, and data matrix (based on Willan, 1987).

TAXON LIST

Gastropoda
Heterobranchia
Opisthobranchia
Notaspidea
Umbraculacea
Fam. Tylodinidae
Tylodina - present, external, uncalcified
Anidolyta - present, external, uncalcified
Fam. Umbraculidae
Umbraculum - present, external, calcified
Pleurobranchacea
Fam. Pleurobranchidae
Subfam. Pleurobranchinae
Pleurobranchus - present, internal, uncalcified
Berthella - present, internal, uncalcified
Bathyberthella - present, internal, uncalcified
Pleurehdera - reduced, internal, uncalcified
Berthellina - reduced, internal, uncalcified
Subfam. Pleurobranchaeinae
Pleurobranchella - absent
Pleurobranchaea - absent
Euselenops - absent

CHARACTER LIST

0. Dummy all-zero.
1. Shell: 0, present; 1, absent (coding reversed).
2. Shell: 0, external; 1, internal.
3. Shell: 0, calcified; 1, uncalcified.
4. Periostracum: 0, smooth; 1, rough or lamellate.
5. Muscle scar: 0, incomplete; 1, intermediate suspensor present; 2, complete.
6. Shell shape: 0, circular; 1, rectangular.
7. Shell location: 0, central; 1, anterior; 2, posterior (Willan character 9, coding adjusted).
8. Shell size relative to body size: 0, large; 1, medium; 2, small (Willan character 10).
9. Shell size relative to mantle size: 0, subequal; 1, mantle larger than shell (Willan character 11).
10. Mantle: 0, smooth; 1, pustulose; 2, puckered (Willan character 12).
11. Mantle spicules: 0, absent; 1, present (Willan character 13).
12. Mantle border, anteriorly: 0, entire; 1, weakly emarginate; 2, deeply cleft (Willan character 14).
13. Mantle margin: 0, entire; 1, slightly crenulate; 2, deeply serrate (Willan character 16).
14. Mantle and oral veil: 0, separate; 1, fused (Willan character 18).
15. Oral tentacles: 0, separate; 1, joined by oral veil (Willan character 21).
16. Oral veil width relative to body: 0, very narrow; 1, narrow; 2, moderately broad; 3, very broad (Willan character 22).
17. Oral veil papillae: 0, absent; 1, present along anterior edge (Willan character 23).
18. Rhinophores: 0, separated; 1, together, unfused; 2, together, fused (Willan character 24).
19. Pedal gland: 0, absent; 1, present (Willan character 27).
20. Gill location: 0, well back, posterior right; 1, posterior right; 2, from left corner to posterior midline (Willan character 31).
21. Gill attachment, extent: 0, half length; 1, less than half length; 2, almost entire length (Willan character 32).
22. Gill rachis: 0, smooth; 1, pustulose (Willan character 33).
23. Anus relative to gill basement membrane: 0, at middle; 1, in front of hind end; 2, above hind end; 3, well behind gill (Willan character 34).
24. Median buccal gland: 0, absent; 1, present (Willan character 38).
25. Radular rachidian teeth: 0, present; 1, absent (Willan character 39; coding reversed).
26. Radular lateral teeth, denticle at base: 0, absent; 1, present (Willan character 40).
27. Radular lateral teeth: 0, not lamellate; 1, lamellate (Willan character 42).
28. Labial cuticle: 0, two separate thickenings (jaws); 1, continuous thickened ring (Willan character 43; coding reversed).
29. Mandibular elements: 0, oval or polygonal; 1, cruciform (Willan character 44; coding reversed).
30. Mandibular elements, blades: 0, denticulate; 1, smooth (Willan character 45; coding reversed).
31. Reproductive condition: 0, monaulic; 1, diaulic; 2, triaulic (Willan character 46).
32. Penial autospermal groove: 0, present; 1, absent (Willan character 48; coding reversed).
33. Penis location: 0, at base of right oral tentacle; 1, anterior midline; 2, on right side in front of gill (Willan character 49; coding adjusted).
34. Penis: 0, non-protrusible; 1, protrusible (Willan character 50).

(Continued)

Table 2. (continued)

35. Allosperm receptacles: 0, two; 1, one (Willan character 52; coding reversed).
36. Receptaculum seminis, origin: 0, low; 1, high (Willan character 53; coding reversed).
37. Prostate gland: 0, surrounding autosperm canal; 1, absent; 2, present as distinct organ (Willan character 54; coding adjusted).
38. Penial gland: 0, absent; 1, present (Willan character 55).
39. Penial sack: 0, absent; 1, present (Willan character 56).
40. Vas deferens, coiling within penial sack: 0, absent; 1, present (Willan character 57).

Notes: Changes to Willan's original coding were:
1. Autapomorphies were removed (characters 7, 15, 19, 20, 25, 26, 28, 30, 35, 36, 41, 47, and 51).
2. Inexplicably, some character states were originally numbered 0-1-2-etc., while others were numbered 1-2-3-etc. The latter characters (3, 5, 8-12, 14, 16, 17, 22, 24, 31-34, 39, 40, 45, 46, 49, 52, 54, and 55) were renumbered here so that the most plesiomorphic state was 0. With this accomplished, character 17 became all 0's, so was eliminated here.
3. In comparing the original coding scheme (Willan, 1987: table 4) with the character list (including plesiomorphic and apomorphic states), some of Willan's apomorphic character states were found inappropriately coded as 0. Coding was here adjusted (usually simply reversed) for characters 1, 9, 37, 39, 43, 44, 45, 48, 49, 52, 53, and 54. Following this recoding, character 37 became an autapomorphy and was eliminated.
4. Some taxa were originally listed as having multiple character states. These were coded here with the most plesiomorphic state. When this was done, characters 8 and 29 became all 1's and dashes (inapplicable), so were eliminated.
5. A probable error was noticed in one of the original shell characters (character 3, shell calcified/uncalcified), where the text claimed "only *Umbraculum* calcifies its shell to any degree" (Willan, 1987: 220) while *Umbraculum* and all other taxa except *Pleurobranchus* and *Bathyberthella* were originally coded as uncalcified. This character was recoded here according to Willan's statement, with the outgroup and *Umbraculum* as calcified (0) and all remaining taxa as uncalcified (1; although Marcus, 1985, noted that the shell of *Tylodina* includes a calcified part); the last three taxa in the matrix were coded here as "inapplicable" (-).
6. An all-zero outgroup was used, and an all-zero character 0 was added.

DATA MATRIX

Outgroup	0000000000000000000000000000000000000000
Tylodina	0001010000000001000000200101—00201-0000
Anidolyta	0001100000000101000000201011—10201-0000
Umbraculum	0000120010000200—10220301001—01—2000
Berthella	0011001000011001102111001100011210111100
Pleurobranchus	0011001000212001102111121100010110111000
Berthellina	0011001121010001102011021101011210100010
Pleurehdera	00110011110-0001102111021111010210101010
Bathyberthella	0011001000000001102111021100000210101000
Pleurobranchella	01--------10-0112100110111000011011-2011
Pleurobranchaea	01--------10-0112101110110000011011-2011
Euselenops	01--------00-0113101111111000011101101000

synapomorphic for Pleurobranchaeinae (Figs. 15-17). Shell reduced (character 9 = Willan's character 11 = 1) was a consistent synapomorphy for the *Berthellina* + *Pleurehdera* clade, and was never prerequisite to shell loss (consistently a branched character state tree as in that given for Figs. 3-8). Shell internalization (character 2 = 1) was synapomorphic for Pleurobranchinae, but the sister clade, Pleurobranchaeinae, was coded "?" for this character, so the character state change could be a synapomorphy for Pleurobranchacea (Figs. 15-17, arrows). Shell decalcification (character 3 = 1) was less definitive, occurring below *Tylodina* in all top-region topologies (and synapomorphic for a large clade above *Umbraculum* in two topologies, Figs. 13-14), but requiring reversals in *Umbraculum* in two topologies (Figs. 11-12).

Binary Coding and Multistate Unordered Coding. These two analyses produced 12 MPTs of 76 steps (CI 0.72, RI 0.73). The Multistate Unordered Analysis combined characters 1 and 9 into one character: 0 = present (and subequal in size relative to mantle), 1 = reduced (in size relative to mantle), and 2 = absent. This replaced character 1, and character 9 was eliminated from the data matrix.

Multistate Ordered Coding. This analysis used the same data matrix as Multistate Unordered Coding, but the analysis was run with character 1 (only) ordered. The resulting 12 MPTs were of 77 steps (CI 0.71, RI 0.73).

Uncoded/Mapped. This analysis used the binary dataset in Table 2 but with characters 1 and 9 deactivated within Hennig86. The resulting 12 MPTs were of 74 steps (CI 0.71, RI 0.72).

Summary. Regardless of coding alternative, there was no change in resultant topologies using the notaspidean dataset (although the tree length and statistics did vary slightly). Interpretation of monophyletic clades and evolution of shell reduction/loss therefore did not change either.

SIGMURETHRAN PULMONATES

Like opisthobranchs, pulmonates include representatives with full, reduced, or absent shells; those with reduced shells are called either semislugs or slugs according to degree of reduction of the visceral mass (slugs having completely internalized shells, and semislugs having external shells that are too small to retract into; T. Pearce, pers. comm.; those lacking shells are also called slugs; Solem, 1974). Unlike in opisthobranchs, however, the degree of shell reduction does not play a traditional role in classification. The shells of land slugs have been judged of limited taxonomic value because of their variability (Reuse, 1983), and because of the convergence "inherent in" reduced shells (Solem, 1978). Terrestrial gastropods therefore present a similar-but-different case for this analysis.

Unfortunately, no robust phylogenetic analysis including a dataset involving all shell morphotypes (present/reduced/absent) suitable for this manipulation has been published. The best available data come from Tillier's (1989) massive anatomical monograph of Stylommatophora, which presented character coding for taxa that were translatable into a data matrix for this demonstration. Tillier's work included nearly 200 taxa (Tillier, 1989: appendix A), but only 17 characters (Tillier, 1989: appendix E) from relatively few organ systems (digestive, excretory, and nervous). To reduce the data matrix to more-normal proportions of characters and taxa, a subset of taxa was chosen for this analysis. Solem (1974) noted that only the Sigmurethra includes fully shelled forms, semislugs, and slugs, so for this analysis, representatives of the sigmurethran subgroup Aulacopoda were selected from Tillier's data. The final dataset included two suprafamilial groups, six families, and 22 genus-level ingroup taxa plus an all-zero outgroup (Table 3). Of the six families, one contains snails only, three contain snails plus either slugs or semislugs (or both), and two contain slugs or semislugs only. Tillier's 17 original characters (Tillier, 1989: appendix E; as clarified by Emberton and Tillier, 1995) were transformed into cladistic characters as noted in Table 3 (see Notes).

No shell reduction character was originally coded by Tillier, although taxa were indicated as "semislug" or "slug" where applicable (Tillier, 1989: appendix B). For this analysis, four character states were used to code the shell as: fully present, reduced (semislug), reduced (slug), and absent (determined in part from familial descriptions in Boss, 1982). Two reduced categories were used to preserve the distinction between the shells of semislugs and slugs, assuming (perhaps in oversimplification) that the shell's condition in slugs is further reduced from that in semislugs. The lists of taxa (22) and characters (20, with shell reduction in binary form) and the data matrix appear in Table 3.

Hennig86's algorithm, *mhennig** (multiple passes without branch-swapping), was used for all analyses (more robust algorithms completed, but produced extraordinarily large numbers of trees). Because of the extreme variability in the results of this analysis, repeating topologies could not be identified. In general, suprafamilial and familial groups were not supported, and because the focus of this demonstration lies in the pattern(s) of character evolution implied by the various results, only examples and character state trees will be presented.

Binary Coding. Analysis of the dataset produced a single MPT (Fig. 18) of 76 steps (CI 0.46, RI 0.57). Shell reduction (character 2 = 1 or 2) occurred in parallel three times. Two of these paths were direct unmodified changes to slug- (character 2 = 2) or semislug-type (character 2 = 1) reduction. The third was a path through semi-slug type reduction to two changes to slug-type reduction and one to shell loss (character 1 = 1).

Multistate Unordered Coding. This analysis combined binary characters 1 and 2 to form a single multistate shell character: 0 = present, 1 = reduced (semislug), 2 = reduced (slug), 3 = absent. The combined character replaced character 1; character 2 was eliminated. The algorithm produced a single MPT of exactly the same topology, length, and statistics as that produced in Binary Coding (Fig. 18).

Multistate Ordered Coding. This analysis used the same modified dataset as Multistate Unordered Coding, but the analysis was run with character 1 (only) ordered. This scenario thus presupposed that shell reduction occurs in this lineage in the following linear order: semislug (reduced) to slug (reduced) to shell absent. The analysis produced seven MPTs of 77 steps (CI 0.45, RI 0.57). Six of the seven trees produced a character state tree and topology similar to that in Fig. 19. The character state tree reflected the linear ordering, but included one reversal from semislug-type reduction back to unreduced. The seventh MPT was similar except lacked the reversal, through relocating the shelled snails to the basal region of the tree.

Uncoded/Mapped. With characters 1 and 2 deactivated from the data matrix in Table 3, a single MPT was produced of 70 steps (CI 0.45, RI 0.55). When mapped on the tree, shell reduction characters produced a generally more complex pattern than in the previous methods (Fig. 20). Reduction occurred three times in parallel, two of these being direct unmodified changes to slug-type reduction. The third pathway was semislug-type reduction leading to slug-type reduction once, shell loss once, and reversals to unreduced shells twice.

Summary. (1) Although Binary and Multistate Unordered Coding produced the same result, Multistate Ordered Coding produced more trees (all different from the previous); Uncoded/Mapped again produced one tree, but again of a unique topology. (2) Suprageneric groups (*i. e.*

traditional superfamilies and families) were inconsistent, therefore monophyletic clades differed drastically depending on coding alternative used. (3) Shell reduction characters formed synapomorphies for at least one multi-taxon clade in all trees, but the supported clades were again dependent upon coding alternative. (4) The hypothesis of evolution of shell reduction and loss (expressed in character state trees) was highly dependent upon coding alternative. Ordering of the character states (unreduced to semislug-type reduction to slug-type reduction to loss) never occurred except when forced by Multistate Ordered Coding.

DISCUSSION

WHAT IS THE "CORRECT" METHOD?

Each of the above trials illustrated four ways of handling one traditional character in a cladistic dataset. The results ranged from differing greatly among methods (pulmonates), to differing slightly (sacoglossans), to not differing at all (notaspideans). The degree of difference corresponded here to what qualitatively appears to be relative strength of the total dataset (especially of non-shell characters therein), expressed by (in pulmonate, sacoglossan, and notaspidean datasets, respectively) (1) the Hennig86 algorithm that would readily resolve (*m**, *m*bb**, and *ie**), (2) range of CI (0.36-0.37, 0.40-0.41, and 0.71-0.72), (3) the amount of overlap among the trial results (very little, some, and total), and (4) the amount of change caused by deactivation of the shell reduction/loss characters (much shorter, but more MPTs; slightly shorter, slightly more MPTs; and no change). Interestingly, one other dataset manipulated in this same manner reacted like the notaspidean dataset - *ie** algorithm, total overlap of results, no change caused by deactivating the character in question. This was the truncatellid gastropod dataset published by Rosenberg (1996), manipulating a gill character originally coded as 0 = present, 1 = reduced, and 2 = absent; this result can also be attributed to the strength of the original dataset.

Binary versus Multistate Coding. Hauser and Presch (1991) theorized that an unordered analysis containing multistate characters should produce exactly the same results as a binary analysis. This was universally true here for all three datasets.

Binary coding of shell reduction/loss characters requires the use of missing character states (= unknown or inapplicable question marks) in the dataset. According to the literature, these can increase the number of MPTs (Wilkinson, 1995) or can cause other missing-data problems attributed to long-distance influence (Maddison, 1993). However in these test datasets, the presence of "?"s did not appear to induce problems, perhaps because these were "safe circumstances" as described by Maddison (1993: 579) where the "inapplicable" regions of the trees were confined to a single taxon (pulmonates) or clade (sacoglossans and notaspideans).

Other arguments against Binary Coding include: (1) binary characters could be redundant or not completely independent (Pimentel and Riggens, 1987; Maddison, 1993), and (2) if there is in fact evidence for an ordered transformational character, this evidence will be forfeited through binary coding and can be lost to the result (Pogue and Mickevich, 1990; Lipscomb, 1994).

Ordered versus Unordered. Hauser and Presch (1991) reanalyzed 27 published datasets to test the results of ordered versus unordered characters; their ordered analyses affected all multistate characters in each dataset, rather than only one as in the test cases here. In agreement with their results, ordering did not demonstrably improve clade resolution, and the number of trees was not necessarily reduced by ordering. Slowinski (1993) reanalyzed 21 published matrices and found similar results: unordered analyses resulted in overall greater resolution and greater congruence. Hauser and Presch (1991: 253) noted that "the effect of ordered characters ... is, in part, based on their interaction with other characters in the datamatrix" so that each individual change to a dataset affects multiple levels. Nevertheless, achieving the best resolved and smallest number of trees out of a dataset is not acceptable rationale for ordering characters. Ordering restricts possible character state transformations and requires independent, corroborating evidence that such a pattern occurred (or that others did not) (*i. e.* ontogeny; Hauser and Presch, 1991).

Slowinski (1993) noted that linear ordering (the most common method) does not always convey the best possible assumption of transformation for multistate characters with four or more states. Here, linear ordering of the shell reduction/loss multistate character in the pulmonate dataset (Fig. 19) presupposed that semislug-type shell reduction preceded slug-type reduction, which in turn preceded shell loss. In all other pulmonate results (Figs. 18, 20), this was not the case as evidenced by branched character state trees; shell loss was most often preceded only by semislug-type reduction.

Choosing an unordered analysis, or "letting the algorithm decide," clearly makes the fewest *a priori* assumptions, and will in fact reveal an ordered transformation series if it is part of the MPT(s). Mickevich and Weller (1990) agreed in part (advocating ordering in general), noting that the pattern of character state change revealed by an unordered analysis can test the validity of a hypothetical ordered transformation series. In the case of the sacoglossan analysis here, the 26 MPTs produced by ordering were a subset of those (56) produced by unordering; the ordered transformation was present in the two most frequently-

Table 3. Sigmurethran pulmonate taxon list (with shell condition), character list, and data matrix. Generic abbreviations (also used in Figs. 18-20) derived from superfamilial group, family, and genus names. Families and generic contents of families are as according to Vaught (1989); suprafamilial groupings are as according to Boss (1982) and South (1992)

TAXON LIST

Gastropoda
Pulmonata
Sigmurethra
Aulacopoda
Arionoidea
Fam. Arionidae
Hemphillia (ArArHm) - reduced, semislug
Aphallarion (ArArAp) - reduced, slug
Oopelta (ArArOo) - reduced, slug
Fam. Philomycidae
Philomycus (ArPhPh) - absent, slug
Fam. Endodontidae
Thaumatodon (ArEnTh) - present, snail
Phrixgnathus (ArEnPh) - present, snail
Limacoidea
Fam. Helicarionidae
Hemiplecta (LiHeHe) - present, snail
Microparmarion (LiHeMi) - reduced, semislug
Cystopelta (LiHeCy) - reduced, semislug
Mariaella (LiHeMa) - reduced, slug
Fam. Urocyclidae
Trochozonites (LiUrTr) - present, snail
Trochonanina (LiUrTc) - present, snail
Acantharion (LiUrAc) - reduced, semislug
Mesafricarion (LiUrMe) - reduced, semislug
Atoxon (LiUrAt) - reduced, slug
Elisolimax (LiUrEl) - reduced, slug
Fam. Zonitidae
Trochomorpha (LiZoTr) - present, snail
Zonites (LiZoZo) - present, snail
Phenacolimax (LiZoPh) - reduced, semislug
Vitrinopsis (LiZoVi) - reduced, semislug
Daudebardia (LiZoDa) - reduced, slug
Plutonia (LiZoPl) - reduced, slug

CHARACTER LIST

0. Dummy all-zero.
1. Shell: 0, present; 1, absent.
2. Shell: 0, fully present; 1, reduced (semislug); 2, reduced (slug).
3. Buccal mass (BM): 0, spheroidal to ovoidal tending toward cylindrical (BM1); 1, clearly cylindrical (BM2).
4. Esophageal crop (OC): 0, absent (OC1); 1, separated from gastric crop by distinct portion of esophagus (OC2); 2, separated from gastric crop by simple constriction (OC3); 3, as in OC3 but extending forward to nerve ring (OC4).
5. Gastric crop (SC): 0, cylindrical (SC1); 1, median portion inflated (SC2); 2, funnelform, widening from esophagus to stomach (SC2'); 3, anterior region inflated (SC3).
6. Gastric pouch (PS): 0, joining gastric crop without any constriction, distinctly wider than crop (PS1); 1, joining gastric crop without any constriction, slightly wider or no wider than crop (PS2); 2, separated from gastric crop by constriction, distinctly wider than crop (PS2').
7. Intestine length (IL): 0, intestinal loops long, reaching level between distal limit of gastric pouch and middle of gastric crop (IL1); 1, intestine shorter, but loops distinct (IL2); 2, intestinal loops long, reaching proximally at least to level of distal limit of gastric pouch (IL2'); 3, intestinal loops reduced to almost flat sigmoid (IL3).
8. Ratio of kidney length:lung length (LR): 0, very short kidney, 0.45-0.7 (LR1); 1, 0.36-0.45 (LR2); 2, 0.7-1.0 (LR2'); 3, 0.25-0.36 (LR3); 4, very long kidney, 0.0-0.25 (LR4) [slugs and semislugs not scored, fide Emberton & Tillier, 1995: 203].
9. Degree of closure of ureter (UR): 0, no closed retrograde ureter = complete mesurethry (UR1); 1, closed ureter reaching at most lung top (UR2); 2, ureteric tube reaching point between lung top and pneumostome (UR3); 3, ureteric tube reaching pneumostome = fully closed = complete sigmurethry (UR4).
10. Internal morphology of kidney (RR): 0, either two distinct regions (distal one usually lacking lamellae) or three distinct regions (median one either lacking lamellae or with lamellae different in appearance from those in proximal) (RR1); 1, kidney homogenous in internal morphology, with lamellae reaching distal region and level of kidney pore (RR2).
11. Cerebral commissure length (CC): 0, greater than 1.1 times right cerebral ganglion width (CC1); 1, 0.9-1.1 times right cerebral ganglion width (CC2); 2, less than 0.9 times right cerebral ganglion width (CC3).

(Continued)

Table 3. (continued)

12. Right cerebropedal connective length (CPD): 0, longer than twice right cerebral ganglion width (CPD1); 1, 1-2 times right cerebral ganglion width (CPD2); 2, shorter than right cerebral ganglion width (CPD3).
13. Ratio of lengths of left:right cerebropedal connectives (CPR): 0, < 0.9 (CPR1); 1, 0.9-1.1 (CPR2); 2, 1.1-1.5 (CPR3); 3, 1.5-2.5 (CPR4).
14. Right pleural ganglion position (PLD): 0, closer to pedal than cerebral ganglion = hypoathroid (PLD1); 1, closer to cerebral than pedal ganglion = epiathroid (PLD2).
15. Left pleural ganglion position (PLG): 0, closer to pedal than cerebral ganglion = hypoathroid (PLG1); 1, closer to cerebral than pedal ganglion = epiathroid (PLG2).
16. Visceral ganglion position relative to median plane of pedal ganglia (VG): 0, on right side (VG1); 1, in middle (VG2); 2, on left side (VG3).
17. Right parietal and pleural ganglia (PAD): 0, separate (PAD1); 1, in contact or fused (PAD2).
18. Left parietal ganglion position (PAG): 0, in contact with left pleural, or closer to it than to visceral ganglion, and separated from both by distinct connective (PAG1); 1, closer to visceral than to left pleural ganglion, and separated from both by distinct connective (PAG2); 2, in contact with visceral ganglion only, and separated from left pleural by distinct connective (PAG3); 3, in contact or fused with both left pleural and visceral ganglia (PAG4).
19. Fusion of visceral ganglion (FG): 0, none (FG1); 1, with right parietal ganglion (FG2); 2, with left parietal ganglion (FG2'); 3, with both parietal ganglia (FG3).

Notes: Tillier's characters (Tillier, 1989: appendix E; as clarified by Emberton and Tillier, 1995) were transformed:
1. by changing original 1-2-2'-3 character codes (reflecting ordered character state changes, with primed states indicating branched character state trees) into linear 0-1-2-3 cladistic character states.
2. by coding any 0-states in the original matrix (unexplained by Tillier and called "eliminated" by Emberton and Tillier, 1995) as "-."
3. where more than one representative per genus was coded by Tillier, by combining them and choosing the most plesiomorphic state (but never "-") for the cladistic data matrix.

DATA MATRIX

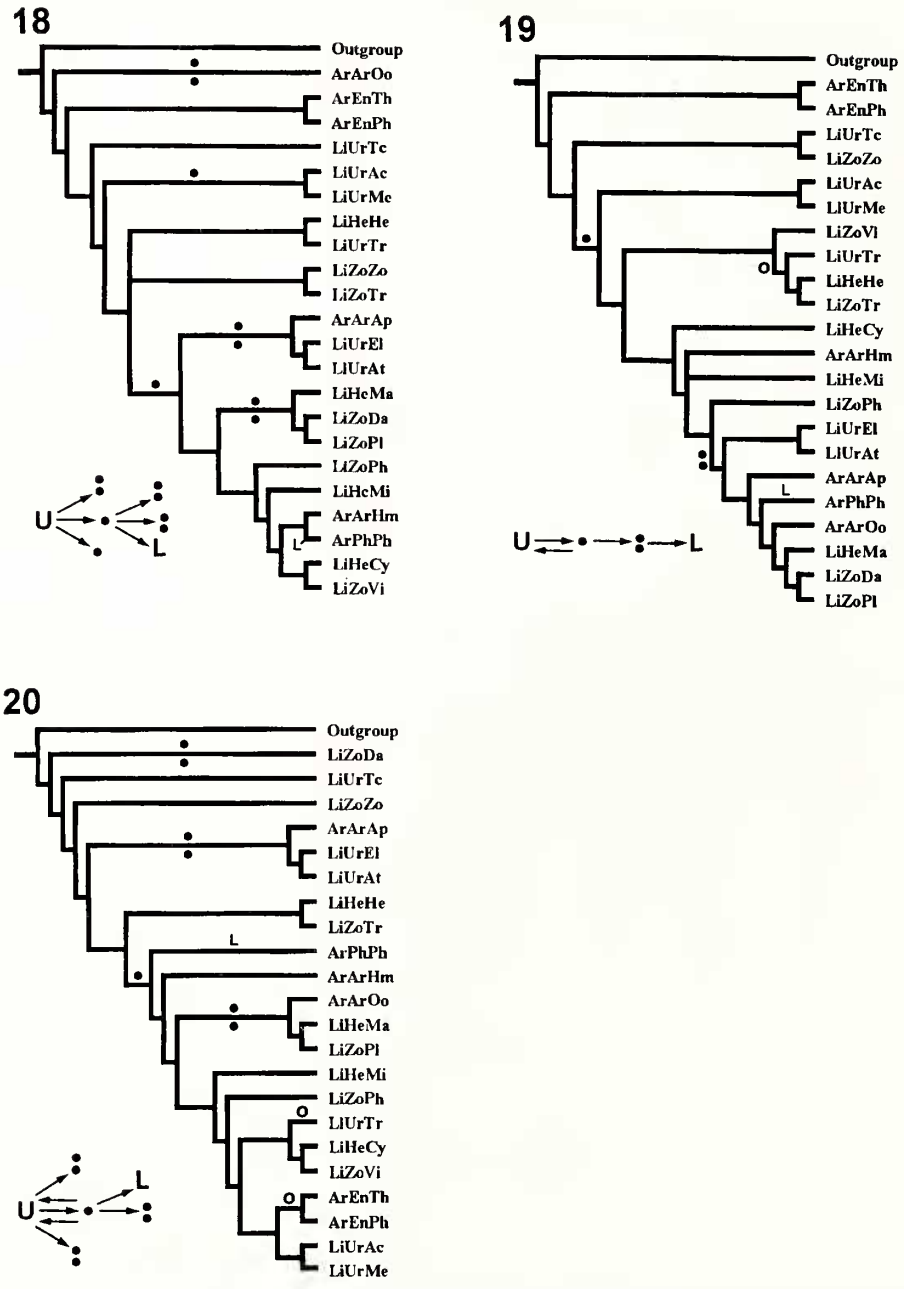
Outgrp	00000000000000000000
ArArHm	00100311-31121000123
ArArAp	00200002-31- - - - - - - -
ArArOo	00200000-31010000122
ArPhPh	01-00000-31221- - -1123
ArEnTh	00000311-10110110001
ArEnPh	00000301330212100101
LiHeHe	00000001230221001120
LiHeMi	00102-01231222 - 00133
LiHeCy	00100001-30220 - - 0133
LiHeMa	00202111231- - - - - - - -
LiUrTr	00000001130222000120
LiUrTc	00000001030110001130
LiUrAc	00102300230211000131
LiUrMe	00102300 - - -211001130
LiUrAt	00203 -12 - 31221001130
LiUrEl	00203 - 12231- - - - - - - -
LiZoTr	00000201230221111110
LiZoZo	00000201031201001130
LiZoPh	00100001- 31222001131
LiZoVi	00100001230 - - - - - - - -
LiZoDa	00210111- - -000001011
LiZoPl	00210111 - 31212002122

occurring topologies and 46% of the MPTs. Ordering only eliminated possible topologies from consideration.

Uncoded/Mapped Characters. *A posteriori* mapping of characters that one deems unusable is also *a priori* reasoning - these characters have been judged beforehand to play no role, or a conflicting role, in evolution of the group. If total evidence (usually combining molecular plus morphological characters in a single dataset) is the best accepted method of determining phylogenetic relationships (Kluge, 1989; de Queiroz *et al.*, 1995), then the same should also be preferred at the morphological level, *i. e.* incorporating as many morphological characters (including negative gain characters) as possible.

TRANSFORMING PHYLOGENETIC ANALYSES INTO CLASSIFICATIONS

Revising taxonomic classification is usually not the sole (nor primary) question being approached using cladistics. Nevertheless, it is always tempting to translate resultant tree(s) following an analysis. Much of the discussion



Figs. 18-20. Pulmonate test dataset results, sample most-parsimonious cladograms and character state trees. Fig. 18. Binary and Multistate Unordered Coding. Fig. 19. Multistate Ordered Coding. Fig. 20. Uncoded/Mapped. See Table 3 for taxon abbreviations. (•, semislug-type reduction; ••, slug-type reduction; o, reversal to unreduced shell; L, shell loss; U, unreduced shell).

here might have centered on differences in, for example, the number of superfamilies required by one cladogram over another. But, abandoning taxonomic rank (as suggested by de Queiroz and Gauthier, 1992; Ponder and Lindberg, 1997; Roth, 1997), at least above ICZN-regulated family-level (ICZN, 1985), renders this discussion irrelevant. Above family-level, it is possible to refer to a clade without worrying about whether it is, for example, a subclass or an order. Abandonment of rank furthermore eliminates the need to erect meaningless "redundant categories" (reviewed by de Queiroz and Gauthier, 1992), *e. g.* an order Cylindrobullacea and family Cylindrobullidae for the monotypic clade defined only by the genus-level synapomorphies of *Cylindrobulla* (Jensen, 1996b).

If one chooses to do so, the number of recognized taxa derived from a cladogram depends on monophyletic

clades (not grades or paraphyletic taxa; Bieler, 1990). As shown by these experimental manipulations, the choice of coding alternative can affect this result. Deciding which monophyletic clades to recognize is still a subjective step, and depends on synapomorphies and other node-defining character state changes. For example, in the sacoglossan trials, Placobranchacea was consistently supported here. Some of the resultant topologies resulted in a large number of taxa at a level equivalent to Placobranchacea, *e. g.* from Fig. 2: *Ascobulla, Volvatella*, Juliidae, and Oxynoidae. But whether these are recognized as five monophyletic clades, or four (*Ascobulla, Volvatella*, Juliidae, Oxynoidae + Placobranchacea), or three (*Ascobulla, Volvatella*, Juliidae + Oxynoidae + Placobranchacea), or two (*Ascobulla, Volvatella* + Juliidae + Oxynoidae + Placobranchacea), or one (all five combined) depends on at which node(s) sufficient support is recognized.

If a cladogram such as that in Fig. 2, suggesting a drastically new classification, is chosen as the preferred tree, the degree of confidence placed in the dataset and its coded characters should determine how to proceed. Is this a robust analysis, with strong corroborating support (*e. g.* high bootstrap or other statistical values; large number of characters), and where the cladogram shows little change with each added character or taxon? Or is this preliminary, with a cladogram that is likely to change topology dramatically as new data are obtained? If the former, then the result must be trusted, regardless of how closely the cladogram agrees with traditional classification or an initial hypothesis of the "true tree." If the latter, then construction of a hierarchial classification should be postponed awaiting further data.

CONCLUSIONS

1. Choosing characters and how to code them is the fundamental step in cladistics - and one not without subjectivity. Precise definition of negative gain characters, such as shell reduction and loss, is critical, requiring more "diligen[ce] in the detail and consistency of terminology" (Proctor, 1996: 145) than in the case of positive gain characters. How to code such characters is equally critical, and as was shown, different coding alternatives can (although not always) produce different cladograms, which can be translated into different classifications - a point made earlier by Pogue and Mickevich (1990).

2. How a data matrix is analyzed is less critical, and it is not the goal of this paper to recommend one method over another. Although Multistate Unordered Coding might be interpreted as having the most support (Pimentel and Riggens, 1987), in the absence of theoretical or procedural preference, the best alternative is to use multiple methods (agreed by Hauser and Presch, 1991; Kim, 1993; but not by Wilkinson, 1992) at least during the iterative stage of character development. As noted by Kim (1993: 335), "agreement among trees estimated by different methods lends greater credibility to the estimates." Ponder and Lindberg (1997) used this approach, including recoding of multistate characters in their dataset as binary characters. This is comparable to the method commonly used as an alternative to total evidence - running separate analyses of molecular versus morphological (*e. g.* Hillis *et al.*, 1996; Shaffer *et al.*, 1997) or behavioral versus morphological data (*e. g.* Prum, 1990), and comparing results generated by the different methods, perhaps also in combined format.

3. Homoplasy should be hypothesized from a phylogenetic analysis, not initially assumed. Negative gain characters, such as shell reduction and loss, have a high likelihood for homoplasy and as such might be preconceived as less informative than positive gain characters in a cladistic analysis. However, Sanderson and Donoghue (1996) showed that homoplasy in a cladogram (resulting in a low CI) can co-occur with a high level of confidence (expressed in that case by high bootstrap support values), which means that potentially homoplastic characters need not automatically be omitted.

Furthermore, homoplasy does not necessarily indicate error or noise. Numerous parsimony-based analyses present high levels of homoplasy (Sober, 1992; Foley, 1993), and many authors have considered homoplasy to "constitute the majority of evolutionary change during the course of evolution and diversification of lineages" (Armbruster, 1996: 227; see also Hennig, 1966, 1983; Gosliner and Ghiselin, 1984; Sluys, 1989b; Moore and Willmer, 1997). Parallelism is often invoked in interpretation of cladograms (*e. g.* Tassy, 1988; Sluys, 1989a; Erséus, 1990; Griswold, 1993; Jensen, 1996b; Salvini-Plawen and Steiner, 1996), absences are presented as synapomorphies (Ax, 1987; Müller and Wagner, 1991), and homoplasy occurs in nearly every cladistic study; in a reanalysis of 38 published data matrices, Maddison (1991: table 2) obtained consistency indices [CIs] ranging from 0.198-0.808 (mean = 0.515).

Wilkinson (1991) opined that parsimony methods fail not when homoplasy is rampant, but when homoplasy is based on misleading evidence - therefore, careful definition of characters and character states is the key. Cladistics is a tool - albeit a powerful one - in studying molluscan systematics; as such, it can help us study homoplasy. Including a limited number of negative gain characters (in conjunction with sufficient positive gain characters) can serve to highlight homoplasy against a background of homology on the final tree (Platnick, 1977), and is the strongest method of testing hypotheses of loss. A low CI-value does not (nec-

essarily) mean that a final result is poor. In these cases, a homoplastic character is informative as long as its suggested transformation is not biologically impossible.

Armbruster (1996: 240) noted that "homoplasy is common in characters with ecological significance" and "characters of ecological importance are often of little systematic utility." These same statements can be said of shell reduction and loss in the Mollusca: "in virtually every major group of mollusks there are some species in which the shell has become reduced to a remnant" (Solem, 1974: 16). Inclusion of these characters wherever possible in analyses could lead to more rigorous documentation of the number and extent of "trends toward shell loss" throughout the phylum.

4. Revising taxonomic classification is only part of why we do cladistics, and might not be supportable from a given analysis. Cladistic analyses rarely generate fully resolved trees with all monophyletic taxa supported by strong synapomorphies. Several equally supported classifications can often be inferred from a single cladogram (Tassy, 1988), depending on the choice of monophyletic groups. Although new cladistic analyses (or reanalyses) are being regularly produced, a phylogenetic classification of all Mollusca still eludes us. In the interim, we must provisionally accept untested and even paraphyletic taxa in molluscan taxonomy, and avoid proposing unstable classifications that will change with the next analysis.

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